

TOE FUSION IN OSCINES

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Although striking differences in extent of webbing between the toes of nonpasserines are well-known and often used to illustrate adaptation in birds, the degree of connection between the toes in oscines has received much less attention. Ridgway (1901-07) in scattered keys and descriptions commented on integumental fusion of the toes of numerous New World oscine taxa, but provided little interpretation on possible significance of the taxonomic variations, apart from their use in distinguishing taxa. Although others (e.g., Rand and Traylor 1953) have occasionally commented on fusion in oscines, a comprehensive survey of the families is lacking. I attempt here to interpret major taxonomic differences in fusion in relation to systematics and behavioral differences and to indicate problems for future study.

MATERIALS AND METHODS

I examined study skins of 1941 species of oscines in the collections of the National Museum of Natural History (Washington, D.C.), American Museum of Natural History (New York), British Museum (Nat. Hist., Tring) and the University of Connecticut. In addition, I made more than 175 observations of toe positions in perching or standing for wild or captive birds representing 30 species. The taxonomic sequence follows Morony, Bock and Farrand (1975).

To examine fusion among the 3 forward toes I used a hand lens or binocular dissecting microscope, except for species of large size. Degree of fusion of the middle (III) and outer (IV) toes is primarily emphasized, but extent of fusion of the inner (II) and middle toes was noted for 349 species, as discussed below. I selected as a major landmark for comparison the articulation between the first and second phalanges of the middle toe, located by bends in that toe, by the plantar flexion creases and, in many cases, by an overlying scute termed the proximal cap (Clark 1977). Fusion of toes III and IV is rated low (L) if not reaching distally to the region of articulation between the first and second phalanges of III, moderate (M) if reaching that region, and high (H) if extending further distally (Fig. 1). These ratings are arbitrary divisions of a continuum, but the extremes of low vs high fusion are markedly different. This summary of fusion in 3 categories provides less detail than sometimes given by Ridgway (1901-07), but is advantageous in facilitating comparisons across a wide range of taxa.

RESULTS AND INTERPRETATION

In tabulating data on fusion of toes III and IV (Table 1), I emphasize particularly the distribution of extreme differences (low vs high) and the condition in many genera considered atypical in their assigned families. Such a summarizing list (Table 1) necessarily obscures many finer taxonomic differences. For example, nearly all genera of the Mimidae have

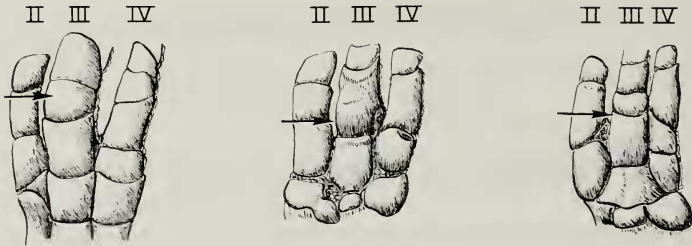


FIG. 1. Examples of toe fusion, from left to right: low, House Sparrow (*Passer domesticus*); moderate, White-breasted Nuthatch (*Sitta carolinensis*); and high, Red-eyed Vireo (*Vireo olivaceus*). The arrows mark the approximate level of the joint between phalanges 1 and 2 of the middle toe.

low fusion, but the inclusion of *Donacobius* extends the mimid range to the moderate level.

Partial associations exist between degree of fusion and behavior. The terrestrial larks (Alaudidae) and pipits (Motacillidae) have low to moderate fusion, whereas many predominantly arboreal Old World families have moderate to high fusion, e.g., Campephagidae, Irenidae, Dicaeidae, Nectariniidae, Zosteropidae, Meliphagidae, Oriolidae, Dicruridae. Families that climb on tree trunks or other vertical surfaces often have moderate to high fusion, e.g., Sittidae, Certhiidae, Climacteridae. Still other Old World families or subfamilies range from low to high fusion, e.g., Laniidae, Timaliinae, Sylviinae, Malurinae. Finches, sparrows and buntings throughout the world (Emberizinae, Cardinalinae, Carduelinae, Estrildidae, Ploceidae) have low to moderate fusion, a level widespread in the New World 9-primaried assemblage, including Parulidae, Drepanididae and Icteridae. However, vireos (Vireonidae), including peppershrikes (*Cyrtarhis*) and shrike-vireos (*Vireolanius*), have greater fusion.

Species within a genus are usually similar in the broad categories of toe fusion used here (Table 1), but a few Old World genera, the warblers *Cettia* and *Bradypterus* and the bush-shrikes *Telophorus*, exhibit exceptional interspecific differences. Within *Cettia*, for example, the low fusion of *C. squameiceps*, *C. major* and *C. brunnifrons* contrasts with high fusion of *C. fortipes*; other species are intermediate. Among the 10 examined species of *Bradypterus*, only *B. seebohmi* has high fusion, the other 9 being low. *Telophorus bocagei*, *T. sulfureopectus*, *T. olivaceus*, *T. nigrifrons* and *T. multicolor* have high fusion in contrast to low to moderate in *T. zeylonus*, *T. viridis*, *T. quadricolor* and *T. dohertyi*. In *Telophorus*, separation of groups of species by degree of fusion matches taxonomic units recognized on other characters (Hall and Moreau 1970), but fusion differences within *Cettia* and *Bradypterus* do not parallel taxonomic

TABLE 1
FUSION OF TOES III AND IV IN OSCINES

Taxa	No. species examined	Fusion ^a
Alaudidae	39	L-M
Hirundinidae	43	L-M
plus		
<i>Atticora</i>	2	H
<i>Neochelidon</i>	1	H
Motacillidae	47	L
Campephagidae	53	M-H
plus		
<i>Chlamydochaera</i>	1	L
Pycnonotidae	12	M-H
plus		
<i>Spizixos</i>	1	L
<i>Hypsipetes</i>	1	L
Irenidae	4	M-H
Laniidae		
Prionopinae	7	M-H
Malaconotinae	24	M-H
plus		
<i>Telophorus</i>	9	L-H
Laniinae	22	L-M
Pityriasinae	1	H
Vangidae	9	H
plus		
<i>Hypositta</i>	1	H
Bombycillidae	6	L
plus		
<i>Phainoptila</i>	1	M
Dulidae	1	M
Cinclidae	5	L
Troglodytidae	20	L-M
Mimidae	12	L-M
Prunellidae	8	L
Muscicapidae		
Turdinae	261	L-M
Orthonychinae		
<i>Orthonyx</i>	2	H
<i>Androphobus</i>	1	H
<i>Psophodes</i>	1	M
<i>Sphenostoma</i>	1	M
<i>Cinclosoma</i>	1	L
<i>Eupetes</i>	1	M
<i>Melampitta</i>	1	L
<i>Ifrita</i>	1	H

TABLE I
CONTINUED

Taxa	No. species examined	Fusion ^a
Timaliinae	38	L-M
plus		
<i>Garritornis</i>	1	H
<i>Stachyris</i>	10	M-H
<i>Rhopocichla</i>	1	H
<i>Macronus</i>	4	M-H
<i>Micromacronus</i>	1	H
<i>Timalia</i>	1	H
<i>Pteruthius</i>	4	M-H
<i>Alcippe</i>	7	M-H
<i>Yuhina</i>	3	M-H
Panurinae	7	L-M
Picathartinae	1	L
Poliophtilinae		
<i>Microbates</i>	1	H
<i>Ramphocaenus</i>	1	H
<i>Poliophtila</i>	2	M
Sylviinae	128	L-M
plus		
<i>Psamathia</i>	1	H
<i>Cettia</i>	9	L-H
<i>Bradypterus</i>	10	L-H
<i>Acrocephalus</i>	21	M-H
<i>Hippolais</i>	3	M-H
<i>Bathmocercus</i>	1	H
<i>Macrosphenus</i>	1	H
Malurinae		
Malurini	12	M-H
plus		
<i>Amytornis</i>	2	L
<i>Stipiturus</i>	1	L
Acanthizini	26	L-M
plus		
<i>Gerygone</i>	5	M-H
Mohouini	3	M-H
Epthianurini	4	L-M
Genus <i>incertae sedis</i>		
<i>Lamprolia</i>	1	M
Muscicapinae		
<i>Bradornis</i>	2	L-M
<i>Melaenornis</i>	3	L-M
<i>Fraseria</i>	1	M
<i>Rhinomyias</i>	2	L-M
<i>Ficedula</i>	15	L-M
<i>Niltava</i>	12	L-M

TABLE 1
CONTINUED

Taxa	No. species examined	Fusion ^a
<i>Muscicapa</i>	14	L-M
<i>Myioparus</i>	2	L-M
<i>Humblotia</i>	1	M
<i>Newtonia</i>	2	M-H
<i>Microeca</i>	4	M-H
<i>Peltops</i>	2	M-H
<i>Petroica</i>	5	L-M
<i>Tregellasia</i>	3	M
<i>Eopsaltria</i>	2	M
<i>Philentoma</i>	1	H
<i>Poecilodryas</i>	4	M-H
<i>Peneothello</i>	1	M
<i>Pachycephalopsis</i>	1	H
Platysteirinae	16	M-H
Monarchinae	54	M-H
Rhipidurinae	22	M-H
Pachycephalinae	34	M-H
plus		
<i>Hylocitrea</i>	1	L
Genus <i>incertae sedis</i>		
<i>Turnagra</i>	1	M
Aegithalidae	7	M-H
Remizidae	7	M-H
Paridae	33	M
Sittidae	22	M-H
Certhiidae	6	M-H
Rhabdornithidae	2	M
Climacteridae	5	H
Dicaeidae	48	M-H
Nectariniidae	94	M-H
Zosteropidae	47	M-H
Meliphagidae	110	M-H
Emberizidae		
Emberizinae	42	L-M
Catamblyrhynchinae	1	M
Cardinalinae	8	L
Thraupinae	24	L-M
Tersininae	1	L
Parulidae	41	L
plus		
<i>Zeledonia</i>	1	L
Drepanididae	11	L-M
Vireonidae	38	M-H
Icteridae	19	L-M

TABLE 1
CONTINUED

Taxa	No. species examined	Fusion ^a
Fringillidae		
Fringillinae	1	L
Carduelinae	17	L-M
Estrildidae	9	L-M
Genus <i>incertae sedis</i>		
<i>Pholidornis</i>	1	M
Ploceidae	15	L-M
Sturnidae	14	L
plus		
<i>Buphagus</i>	1	M
Oriolidae	22	M-H
Dicruridae	17	M-H
Callaeidae	3	L
Grallinidae	4	M
Artamidae	9	M-H
Cracticidae	7	M-H
Ptilonorhynchidae	11	L-H
Paradisaeidae	31	M-H
Corvidae	93	L-M
plus		
<i>Platylophus</i>	1	H
<i>Crypsirina</i>	2	M-H
<i>Temnurus</i>	1	H

^a Symbols: L = low, M = moderate, H = high.

groups of species. Unfortunately, little has been reported about the use of the feet in *Cettia*, *Bradypterus* and *Telophorus*; species of the first 2 are widely noted as difficult to observe as they skulk in brush.

Fusion of toes II and III.—Fusion of toes II and III extends less far distally than that between III and IV. The relatively few taxa with fusion of II and III reaching distally to the vicinity of the articulation of phalanges 1 and 2 of toe III also have high fusion of toes III and IV, e.g., Vangidae, *Orthonyx*, *Microbates*, *Ramphocaenus*, certain muscicapid flycatchers, *Hypositta*, *Certhia*, *Climacteris*, Vireonidae.

Evolution and systematics.—The taxonomic distribution of different degrees of fusion including variation within genera, subfamilies and families shows that evolutionary convergence has been frequent. Among birds as a whole, and among oscines, high fusion between toes is probably usually a derived, rather than primitive, condition. However, reduction of high

fusion remains a hypothetical possibility and might have occurred occasionally. Raikow (1978) suggested that in situations where evolutionarily primitive and derived conditions are indeterminable, systematists should use characters phenetically while recognizing that resulting hypotheses on relationships will be relatively weak. Any systematic suggestions for oscines based heavily on similarity of toe fusion would be at best tentative, but where fusion agrees with other characters in differing markedly between genera traditionally hypothesized to be closely related, reconsideration of affinities seems warranted, as in certain of the following examples.

The monotypic *Chlamydochaera* from Borneo is the sole genus of the cuckoo-shrikes (Campephagidae) with low fusion. Ames (1975) found that *Chlamydochaera* was unique among examined campephagids in having a thrush-like syrinx and concluded that the genus belongs in the thrushes (Turdidae). The low fusion of the toes is also like that of thrushes. In addition, Ames found thrush-like syringes in the muscicapine genera *Bradornis*, *Melaenornis*, *Rhinomyias*, *Ficedula*, *Niltava* and *Muscicapa*, which, unlike most other Old World flycatchers, also have relatively low toe fusion like that of thrushes.

Harrison (1967) suggested that the babbler *Ifrita* from New Guinea is closely related to the blue wren group of *Clytomyias*, *Chenorhamphus*, *Todopsis* and *Malurus* of Australia and New Guinea. I find that all these genera share a high fusion of toes III and IV. In addition, *Ifrita* has a ridged culmen like that of *Clytomyias* and shares the unusual feature of blue feathering on the head with *Todopsis*, *Malurus* and male *Chenorhamphus*. Thus, several characters link *Ifrita* with the malurids, indicating a possible relationship not reflected in traditional classification. *Clytomyias*, *Chenorhamphus*, *Todopsis* and *Malurus* have an unusual gap in the interscapular zone of the spinal feather tract, present also in the Australian grass-wrens (*Amytornis*) and emu-wrens (*Stipiturus*; Harrison 1969); the condition of *Ifrita* in this regard has not been reported. As the relatively terrestrial *Amytornis* and *Stipiturus* have low fusion, caution is necessary in using fusion as a taxonomic character in this group.

Dorst (1960) proposed that the monotypic genera *Tylas* and *Hypositta* from Madagascar belong in the family Vangidae, which is endemic to that island. The high fusion in all these birds is compatible with his suggestion, although high fusion also occurs in other families with which *Tylas* has often been placed, including bulbuls (Pycnonotidae). In *Hypositta*, toe fusion is greater than in typical nuthatches (Ridgway 1904:439; this study), and *Hypositta* is thus more like the vangids in this respect. Also from Madagascar is *Newtonia*, the sole genus of the Muscicapinae outside the Australian region having moderate to high fusion. Although superficial appearances of study skins can be highly misleading concerning evolu-

tionary affinities, *Newtonia brunneicauda* and females of the vangid *Calicalicus madagascariensis* have some resemblance. Further consideration of the affinities of *Newtonia* would be desirable.

The high fusion of *Cyclarhis*, *Vireolanius*, *Vireo* and *Hylophilus* supports the idea that these genera constitute a monophyletic group (Barlow and James 1975, Raikow 1978). Such high fusion is unusual among New World oscines, being known otherwise from *Certhia* and 2 genera of swallows, *Microbates*, *Ramphocaenus*. Vireos thus differ markedly from most New World 9-primaried oscines, including warblers, tanagers, blackbirds and buntings.

Use of the feet.—As relationships between the degree of fusion and use of the feet are not well understood, I have emphasized here the most conspicuous taxonomic differences, for associations between structure and behavior might be most prominent in such cases. My findings support Rüggeberg's (1960) conclusions, based on a much smaller sample of species, that high fusion often occurs in arboreal species and that low fusion is typical for terrestrial species. Bock and Miller (1959) indicated that the high fusion of syndactyly in nonpasserines was advantageous in arboreal perching because the parallel position of the toes applies all the force of flexion directly against a branch; separated toes would presumably be mechanically less efficient. In those climbing oscines with syndactyly, the forward toes are restrained in a roughly parallel orientation that possibly helps to ensure a secure grasp on vertical surfaces.

My observations of live oscines and of published photographs indicate that birds with low fusion vary the spread of the forward toes considerably according to the kind of perch. On the ground or other flat surfaces, these toes are widely separated, presumably providing a stable base for standing or moving. However, on horizontal perches of a small diameter relative to foot size the forward toes are held close together, a position equivalent to that of syndactyly, with presumably similar advantages. On sharply inclined perches of small diameter, toe II of the lower foot is often abducted from III and IV, which are held close together (Leisler 1972; see also Willis 1969, 1972); the application of forces in 2 directions against the perch by toe II, as opposed to III and IV, presumably helps to prevent the foot from slipping down the perch. Leisler (1972) has provided further details on the relationships between toe position and body orientation of small oscines perched on vertical stems.

A lack of absolute associations between degree of syndactyly and use of the feet prevents the use of structure to predict habits of species not studied alive. For example, the climbing Black-and-white Warbler (*Mniotilta varia*) has low fusion, like that of allied nonclimbing parulids (Parkes 1978; this study), in contrast to the moderate to high fusion of many trunk-

climbers in other families. The tree creepers (*Certhia*), which have highly fused forward toes and stiffened tail feathers, are climbers. Because *Orthonyx* from Australia and New Guinea have the same structural characteristics they might be expected also to be climbers: however, *Orthonyx* actually forage terrestrially, propping themselves on the ground with 1 leg and stiffened tail while scratching in the litter with the other foot (Zusi 1978). As another example of absence of absolute associations between toe fusion and degree of arboreality, many arboreal species have only low to moderate fusion, e.g., kinglets (*Regulus*) and New World orioles (*Icterus*). Possibly such arboreal birds with low fusion differ in perching habits from those with high fusion, but evidence is lacking.

Although asynchronous terrestrial gaits (walking and running) are characteristic for terrestrial oscines, and synchronous (hopping) for arboreal species, there are many exceptions (Clark 1975), and degree of toe fusion is not absolutely associated with gait, except that walking is apparently exceptional in oscines with high fusion. Furthermore, no direct association exists between degree of fusion and the ability to hold food with the feet (Clark 1973). Relationships between fusion and uses of the feet may not be apparent in many cases without simultaneously considering many other aspects of structure and behavior.

SUMMARY

The degree of toe fusion, here summarized for the oscine families, probably has only limited taxonomic usefulness, but may serve along with other characters to detect genera possibly needing further systematic study, e.g., *Chlamydochaera*, *Ifrita*, *Newtonia*. Terrestrial species often have lower fusion than do arboreal or climbing species, but there are important exceptions. Low fusion apparently aids balance on flat substrates, whereas high fusion facilitates perching or climbing. The large number of arboreal species with low fusion has not yet been satisfactorily explained.

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SEVENTH INTERNATIONAL CONFERENCE ON BIRD CENSUS WORK AND FIFTH MEETING OF THE EUROPEAN ATLAS COMMITTEE

An international conference for those involved or interested in bird census and/or atlas work will convene 8-12 September 1981 at the Universidad de León, Spain. For further information write: Prof. Francisco Purroy, Departamento de Zoología, Facultad de Biología, León, Spain.